

# Monomer dynamics of a wormlike chain

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**Abstract** – We derive the stochastic equations of motion for a tracer that is tightly attached to a semiflexible polymer and confined or agitated by an externally controlled potential. The generalised Langevin equation, the power spectrum, and the mean-square displacement for the tracer dynamics are explicitly constructed from the microscopic equations of motion for a weakly bending wormlike chain by a systematic coarse-graining procedure. Our accurate analytical expressions should provide a convenient starting point for further theoretical developments and for the analysis of various single-molecule experiments and of protein shape fluctuations.

**Introduction.** – Many of the tools available to an experimental biophysicist probe either the fluctuations of semiflexible polymers or their response to external forces. This includes dynamic light scattering [1, 2], active and passive microrheology of polymer networks [3] or cells [4], magnetic bead twisting cytometry [5], DNA relaxation and stretching [6], single-molecule force spectroscopy [7] and electron transfer techniques [8]. From a theoretical point of view, these methods expose different aspects of the *wormlike chain* (WLC) model. It provides a minimal description of semiflexible polymer physics in terms of an inextensible, thermally fluctuating elastic beam, and has found broad acceptance on grounds of its excellent agreement with experimental data.

Deformations of the polymer contour excite a broad spectrum of bending modes with widely disparate relaxation times, thus resulting in anomalous, subdiffusive dynamics. In the linear regime, valid for equilibrium fluctuations or small external forces transverse to the polymer backbone, the dynamic mean-square displacement of a tagged (but mechanically unaltered) monomer obeys  $\text{MSD}_\perp(t) \propto t^{3/4}$  [9, 10]. For fluctuations parallel to the polymer axis, the additional longitudinal solvent friction induces tension forces which in turn stiffen the polymer and give rise to a different scaling behaviour,  $\text{MSD}_\parallel(t) \propto t^{7/8}$  [11]. Tension also dominates the response to strong point forces and externally imposed solvent flows; the resulting equations of motion are highly nonlinear and can produce a multitude of different dynamical regimes even in the course of a single experiment [12–16].

In many cases of practical interest, a full evaluation of the dynamics would be needlessly complicated and wasteful, since experimental manipulation and data acquisition are strongly localised, say, to an attached tracer particle, or a tagged monomer, in the following simply referred to as “the tracer”. Farther parts of the polymer matter only insofar as they contribute to the force on the tracer. It can then be preferable to integrate out the polymeric degrees of freedom beforehand and subsume them under an effective equation of motion describing the tracer coordinate only. Such a reduced description is for example known for the important special case of a tracer subjected to an externally prescribed deterministic force protocol [16]. It cannot, however, easily be extended to accommodate for the fluctuating forces exerted onto the tracer by an externally controlled confinement potential. Practical examples that involve such a potential are provided by various single-molecule manipulation techniques (think *e.g.* of an actin filament labelled with a gold nanoparticle that is trapped by optical tweezers). The analysis of high-frequency shape fluctuations of globular proteins, as measured by electron transfer techniques [8, 17] provides another important example. Indeed, the WLC has been proposed as one possible model of protein fluctuations, but to date only numerical evaluations of the corresponding noise and friction functions are available within a mean-field approximation to the WLC [20].

In the following, we systematically derive the sought-after reduced equation of motion for the tracer coordinate  $x(t)$ , starting from the WLC in the weakly-bending limit,

which is asymptotically exact for large bending rigidity or strong stretching force. The resulting GLE,

$$\int_0^t d\tau K(t-\tau)\dot{x}(\tau) = F(x, t) + \Xi(t), \quad (1)$$

is not necessarily linear, as it may include an arbitrary external potential  $U(x, t) = -\int dx' F(x', t)$ . In the infinite-length limit  $L \rightarrow \infty$ , the GLE (1) can be worked out explicitly in terms of the microscopic parameters, which comprise the length  $L$  of the polymer, its bending rigidity  $\kappa$ , and tension  $f$ . It is validated by comparison with numerical solutions of the exact equations of motion. We moreover give a simple interpolation formula (9) that provides a universal description for polymer-bound tracer particles in strongly localised externally controlled potentials and possibly also for the mentioned protein shape fluctuations. We expect it to become a valuable and convenient tool for analysing a wealth of experimental data and for future theoretical developments. By providing a physically transparent and concise parametrisation of measured tracer movements, it will moreover be helpful in the mutual comparison of data obtained with diverse experimental techniques. To exemplify our approach, we calculate various observables characterising the time-dependent spatial correlations of the tracer motion, such as its power spectrum and mean-square displacement in presence of a harmonic trap.

**Langevin description of a WLC.** – In the WLC model, a semiflexible polymer is mechanically represented as an inextensible elastic beam of length  $L$  and bending rigidity  $\kappa$ . It follows that thermal forces can only induce significant bending on length scales larger than the *persistence length*  $\ell_p = \kappa/(k_B T)$  (in 3 dimensions). In the weakly-bending limit, valid for large persistence length  $\ell_p \gg L$  or strong external stretching force  $f \gg k_B T/\ell_p$ , the polymer is essentially straight and can thus be treated in terms of its small excursions  $r_\perp(s, t)$  from the straight-rod ground state. The elastic bending energy in a given configuration  $r_\perp(s, t)$  reads [9]

$$\mathcal{H} = \int_0^L ds \left[ \frac{\kappa}{2} (r_\perp'')^2 + \frac{f}{2} (r_\perp')^2 \right].$$

Shape fluctuations of the polymer then obey a Langevin equation obtained by balancing the corresponding bending forces with friction and thermal (Gaussian white) noise [9],

$$\zeta_\perp \dot{r}_\perp = -\frac{\delta \mathcal{H}}{\delta r_\perp} + \xi_\perp = -\kappa r_\perp'''' + f r_\perp'' + \xi_\perp \quad (2a)$$

$$\langle \xi_\perp \rangle = 0 \quad (2b)$$

$$\langle \xi_\perp(s, t) \xi_\perp(s', t') \rangle = 2\zeta_\perp k_B T \delta(t-t') \delta(s-s'). \quad (2c)$$

In the vein of a similar treatment for a Rouse chain monomer [21], we now introduce a tracer at  $s = s_0$  and let

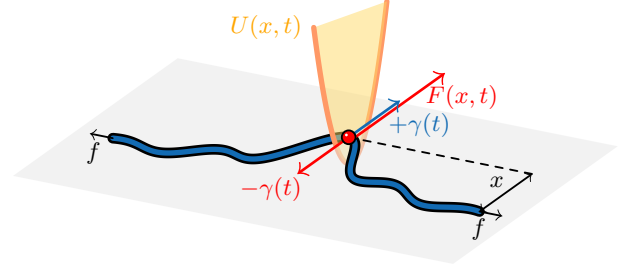


Figure 1: Force diagram for the combined system of a tracer (red) and an attached WLC (blue). The tracer is displaced by an external potential  $U(x, t) = -\int F(x, t) dx$ . The constraining force pair  $\pm\gamma(t)$  fixes the polymer backbone to the tracer position  $x$ .

it absorb the external driving force  $F(x, t)$ ,

$$\zeta_{\text{tr}} \dot{x}(t) = F(x, t) - \gamma(t) + \xi_{\text{tr}}(t) \quad (3a)$$

$$\zeta_\perp \dot{r}_\perp(s, t) = -\kappa r_\perp''''(s, t) + f r_\perp''(s, t) + \gamma(t) \delta(s - s_0) + \xi_\perp(s, t) \quad (3b)$$

$$r_\perp(s_0, t) \stackrel{!}{=} x(t). \quad (3c)$$

Here  $\zeta_{\text{tr}}$  and  $\xi_{\text{tr}}$  denote an optional friction coefficient and Gaussian white noise source for the tracer, respectively. Both may be set equal to zero in the tagged-monomer case. The (Lagrange) forces  $\pm\gamma(t)$  serve to rigidly tie the tracer to the polymer contour at  $s_0$ , as required by the constraint (3c). The latter is simplified by transferring to a comoving reference frame, in which the tracer is always at rest,  $\Delta(s, t) \equiv r_\perp(s, t) - x(t)$ . The corresponding equation of motion acquires a spatially constant friction term due to the drift between the comoving reference frame and the solvent,

$$\zeta_\perp \dot{\Delta}(s, t) = -\kappa \Delta''''(s, t) + f \Delta''(s, t) + \xi_\perp(s, t) + \gamma(t) \delta(s - s_0) - \zeta_\perp \dot{x}(t) \quad (4a)$$

$$\Delta(s_0, t) = 0. \quad (4b)$$

The formal solution for  $\gamma$  can immediately be written down in the frequency domain,

$$\gamma_\omega = - \underbrace{\frac{\int d\sigma \xi_{\perp, \omega}(\sigma) G_\omega(s_0, \sigma)}{G_\omega(s_0, s_0)}}_{\Xi_\omega} - i\omega x_\omega \underbrace{\frac{\int d\sigma G_\omega(s_0, \sigma)}{G_\omega(s_0, s_0)}}_{-K_\omega},$$

where  $G(s, s', t)$  denotes the transverse Green's function of a WLC, *i.e.* its transverse deformation  $r_\perp(s, t)$  in response to a unit force impulse  $\delta(s-s')\delta(t)$ . This explicitly establishes the link between the microscopic equations of motion (2) and the coarse-grained equation for the tracer (1). A practical way of evaluating  $\gamma(t)$  numerically consists in the decomposition of  $\Delta(s, t)$  into its normal coordinates [22]. This procedure is discussed for arbitrary boundary conditions and monomer positions  $s_0$  in the appendix.

**Analytical solution.** – To proceed analytically, we now consider the centre monomer only,  $s_0 = 0$ . Instead

of explicitly including the “adhesion force”  $\gamma(t)\delta(s)$ , which induces a coupling of different eigenmodes and thus renders the dynamics nondiagonal, we can then easily take care of the constraint  $\Delta(0, t) = 0$  by restricting the function space accordingly. Using only those eigenmodes  $\mathcal{W}_n(s)$  satisfying  $\mathcal{W}_n(0) = 0$ , the singular force  $\gamma$  can be read off as follows,

$$\begin{aligned}\kappa\Delta''''(0, t) &= \gamma(t)\delta(s) \\ \kappa(\Delta'''(0^+, t) - \Delta'''(0^-, t)) &= \gamma(t).\end{aligned}$$

Since the above expression vanishes for odd eigenmodes, only even modes  $\mathcal{W}_n(s) = \mathcal{W}_n(-s)$  contribute to  $\gamma$ . Requiring further that  $\Delta''''$  constitutes the highest (and only) singularity, we thus find  $\Delta'(0^\pm) = 0$  and so obtain the following friction kernel,

$$K(t) = 2 \sum_n \mathcal{W}_n''''(0) \frac{\int_0^{L/2} \mathcal{W}_n(s) ds}{\int_0^{L/2} \mathcal{W}_n(s)^2 ds} e^{-\mathcal{E}_n t / \zeta_\perp},$$

where

$$\begin{aligned}\kappa\mathcal{W}_n''''(s) - f\mathcal{W}_n''(s) &= \mathcal{E}_n\mathcal{W}_n(s) \\ \mathcal{W}_n(0) = \mathcal{W}_n'(0) &= 0,\end{aligned}$$

and the outer boundary conditions are dictated by the physical situation. In the infinite-length limit  $L \rightarrow \infty$ , valid for  $t \ll \tau_1$ ,  $K(t)$  becomes independent both of  $s_0$  and of the choice of outer boundary conditions. Using torqued ends  $\mathcal{W}_n'(L/2) = \mathcal{W}_n'''(L/2) = 0$  for convenience, we find

$$K(t) \sim 8 \sum_{n=0}^{\infty} \left[ 8 \frac{n^2 \pi^2 \kappa}{L^3} + \frac{f}{L} \right] e^{-t/\tau_n}. \quad (5)$$

with a relaxation time spectrum

$$\tau_n \sim \frac{\zeta_\perp L^4}{\kappa \pi^4} \frac{1}{(2n)^4 + (2n+1)^2 f/f_L}.$$

Here,  $f_L = \kappa \pi^2 / L^2$  denotes the Euler buckling force. For semiflexible polymers,  $f_L$  is usually small in comparison to externally applied stretching forces. Mode numbers below a critical value  $n_c = (f/f_L)^{1/2}$  are then tension-dominated, whereas shorter-wavelength modes exhibit force-free relaxation and therefore  $\tau_n \propto n^{-4}$ . This divides the frictional response  $K(t)$  to a transverse force into three different asymptotic regimes. At short times  $t \ll \tau_{nc} = \zeta_\perp \kappa / 2f^2$ , the backbone tension can be neglected so that  $K(t)$  simplifies to

$$K(t \ll \tau_{nc}) \sim \frac{2\sqrt{2}\kappa^{1/4}}{\Gamma(1/4)} (\zeta_\perp/t)^{3/4} \quad (6)$$

Between  $\tau_{nc}$  and the terminal relaxation time  $\tau_1$ , we have

$$K(\tau_{nc} \ll t \ll \tau_1) \sim \frac{2}{\Gamma(1/2)} \sqrt{f\zeta_\perp/t}, \quad (7)$$

and at very long times  $t \gg \tau_1$ , the exponential relaxation

$$K(t \gg \tau_1) \propto \begin{cases} e^{-t/\tau_1} & f = 0 \\ e^{-t/\tau_0} & f > 0 \end{cases} \quad (8)$$

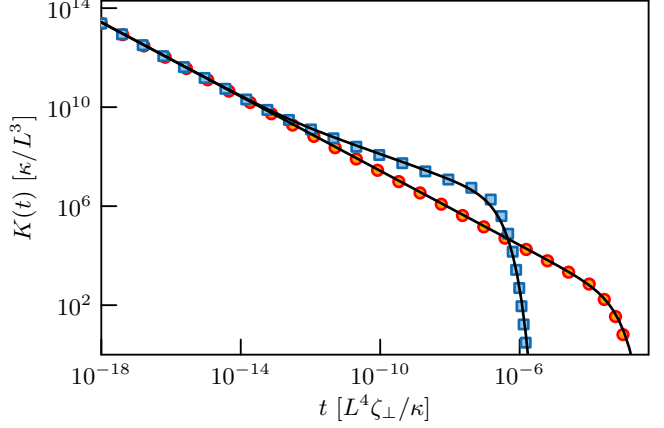


Figure 2: The analytical interpolation formula (9) compared to the exact numerical solutions for  $f = 0$  (○) and  $f = 10^6 f_L$  (□).

of the lowest mode provides a natural physical cutoff of the scale-free intermediate asymptotic dynamics. Using a time-dependent mode cutoff at  $\tau_n = t$ , we arrive at the approximate interpolation formula

$$\begin{aligned}K(t) \approx & \frac{2\sqrt{2}}{3\pi\sqrt{\kappa}} \sqrt{\sqrt{f^2 + 4\zeta_\perp \kappa/t} - f} \\ & \times \left[ \sqrt{f^2 + 4\zeta_\perp \kappa/t} + 2f \right] e^{-t/\tau_*}, \quad (9)\end{aligned}$$

which faithfully reproduces the general solution described in the appendix, see fig.(2).

An exact treatment of the binding constraint (3c) renormalises the terminal relaxation time, which is why we consider  $\tau_*$  as a free (fit) parameter. In the long-polymer limit ( $L, \tau_* \rightarrow \infty$ ,  $e^{-t/\tau_*} \rightarrow 1$ ), eq. (9) reduces to a two-parameter formula.

The associated colored noise term  $\Xi(t)$  of eq. (1) can be determined from the fluctuation-dissipation theorem (FDT),

$$\langle \Xi(t)\Xi(t') \rangle = 2k_B T K(|t - t'|).$$

**Example applications.** — As an example application of our single-coordinate equation of motion eq. (1), we first rederive the time-dependent MSD of a monomer in the bending-dominated regime. We then include an external harmonic potential to compute both the time-dependent MSD and the power spectrum of a polymer-bound tracer particle held in a harmonic trap.

For the free polymer in solution, we set  $F(x, t) = 0$  and hold the tagged monomer fixed until  $t = 0$ . Using the early-time asymptote to  $K(t)$ , eq. (6), its trajectory then follows as

$$x(t) - x(0) \sim \frac{1}{2\sqrt{2}\Gamma(3/4)\kappa^{1/4}\zeta_\perp^{3/4}} \int_0^t \frac{\Xi(\tau) d\tau}{(t - \tau)^{1/4}}, \quad (10)$$

The MSD follows from eq. (10),

$$\text{MSD}_{F=0}(t \ll \tau_{nc}) \sim \frac{1}{2\Gamma(7/4)} \frac{\sqrt{2}k_B T}{\kappa^{1/4}} \left[ \frac{t}{\zeta_\perp} \right]^{3/4}.$$

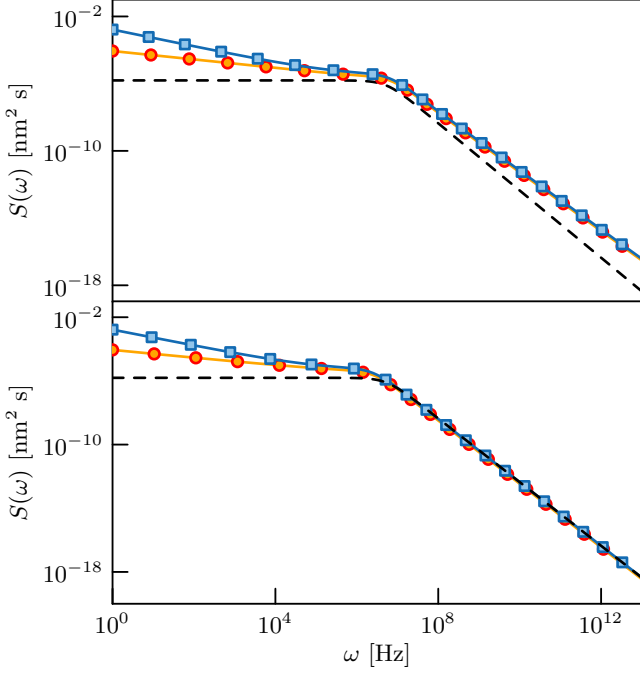


Figure 3: *Top panel*: power spectrum of an unmodified tagged monomer (no excess friction) with  $\ell_p = 10 \mu\text{m}$ ,  $\zeta_\perp = 10 \text{ mPa} \cdot \text{s}$ ,  $k = 1 \text{ pN/nm}$ ,  $T = 300 \text{ K}$ ,  $L \rightarrow \infty$  (*i.e.*  $\omega\tau_* \rightarrow \infty$ ) and  $f = 5 \text{ pN}$  ( $\square$ ),  $f = 0$  ( $\circ$ ). *Bottom panel*: power spectrum of an attached tracer particle that has a perceptible friction coefficient  $\zeta_{\text{tr}} = 6\pi\eta_{\text{water}}r$ ,  $r = 10 \text{ nm}$ , other parameters as above. The Lorentzian power spectrum of the same bead without the attached polymer is shown for comparison (dashed line).

This subdiffusive behaviour coincides with previous theoretical predictions [2] and has been measured directly and indirectly in networks of polymerized actin [1, 10] and microtubuli [5]. Including a stationary harmonic trap of stiffness  $k$ , *i.e.*,  $F(x, t) \equiv F(x) = -kx$ , equation (10) turns into

$$x(t) \sim x(0) \text{E}_{\frac{3}{4}} \left[ \frac{-k(t/\zeta_\perp)^{3/4}}{2\sqrt{2}\kappa^{1/4}} \right] - \frac{1}{k} \int_0^t d\tau \Xi(\tau) \frac{\partial}{\partial t'} \text{E}_{\frac{3}{4}} \left[ \frac{-k(t'/\zeta_\perp)^{3/4}}{2\sqrt{2}\kappa^{1/4}} \right]_{t'=t-\tau}, \quad (11)$$

where

$$\text{E}_\alpha(z) = \sum_{n=0}^{\infty} \frac{z^{\alpha n}}{\Gamma(1 + \alpha n)}$$

denotes the Mittag-Leffler function, which can be regarded as a generalised exponential function. The resulting MSD for  $x(0) \equiv 0$  reads

$$\text{MSD}_{F \neq 0}(t \ll \tau_{n_c}) \sim \frac{k_B T}{k} \left[ 1 - \text{E}_{\frac{3}{4}}^2 \left[ \frac{-k(t/\zeta_\perp)^{3/4}}{2\sqrt{2}\kappa^{1/4}} \right] \right].$$

A deterministic external force  $f_{\text{ext}}(t)$  or a dynamically moving optical trap, represented by  $f_{\text{ext}}(t) \equiv kx_0(t)$ , can be included along the same lines by setting  $F(x, t) =$

$-kx + f_{\text{ext}}(t)$ . Finally, we calculate the power spectrum density for a polymer-bound bead in harmonic confinement,

$$S_\omega = \int_{-\infty}^{\infty} \langle x(t)x(0) \rangle e^{-i\omega t} dt,$$

as measured by video microscopy or other in-plane techniques. (Note that for 3d position tracking  $x$  becomes a 2d vector transverse to the polymer backbone, and  $S_\omega^{3d} = 2S_\omega$ .)

The somewhat lengthy explicit result has a simple structure, suitable for fitting experimental data. Specialising to the infinite-length limit ( $\omega\tau_* \rightarrow \infty$ ), we find

$$\frac{S_\omega}{k_B T} = \frac{4\zeta_\perp R_\omega + 2\zeta_{\text{tr}}}{[k - \omega\zeta_\perp I_\omega]^2 + \omega^2 [\zeta_{\text{tr}} + \zeta_\perp R_\omega]^2} \quad (12)$$

where  $R_\omega$  and  $I_\omega$  denote the real and imaginary parts (with a dimension of length) of

$$2\sqrt{2}\kappa \left[ (f - \sqrt{f^2 + 4i\omega\zeta_\perp\kappa})^{-1/2} + (f + \sqrt{f^2 + 4i\omega\zeta_\perp\kappa})^{-1/2} \right],$$

respectively. For a tracer that causes a perceptible friction ( $\zeta_{\text{tr}} = 6\pi\eta r_{\text{tr}} > 0$ ), the ultimate high-frequency limit is of the usual Lorentzian form  $S(\omega \rightarrow \infty) \sim \omega^{-2}$ . If  $\zeta_{\text{tr}}$  vanishes or is imperceptibly small compared to the monomer friction, the decay of the power spectrum is slightly weaker at large frequencies,  $S \sim \omega^{-7/4}$ . This can intuitively be understood as a consequence of the frequency-dependent “apparent bead size”, given by the subsection (of length  $\ell_\perp$ , where  $\ell_\perp^{-4} \simeq \zeta_\perp \omega / \kappa$ ) of the attached polymer that equilibrates with the bead within one period  $\omega^{-1}$ . See fig. 3 for a graphical representation.

In the absence of backbone tension ( $f = 0$ ), the power spectrum (12) simplifies to ( $s = \sin(\pi/8)$ ,  $c = \cos(\pi/8)$ )

$$\frac{S_\omega^{f=0}}{k_B T} = \frac{8\zeta_\perp^{3/4}(\kappa/\omega)^{1/4}(s+c) + 2\zeta_{\text{tr}}}{[k + 2\kappa^{1/4}(\zeta_\perp\omega)^{3/4}(s-c)]^2 + \omega^2 [\zeta_{\text{tr}} + 2\zeta_\perp^{3/4}(\kappa/\omega)^{1/4}(s+c)]^2}.$$

**Conclusions.** – Starting from the formally exact WLC equation of motion in the weakly-bending rod approximation, we have derived a generalised Langevin equation describing the dynamics of a tagged monomer of (or “tracer” attached to) a semiflexible polymer. The tracer was allowed to be under the influence of an arbitrary external potential. Our method is simple, direct and analytically solvable. We have furthermore derived a uniformly valid analytic interpolation formula which may serve as a compact (two- or three-parameter) parametrisation of, *e.g.*, the motion of a tracer attached to a semiflexible polymer and manipulated by an optical trap, or of conformational fluctuations of protein domains. With regard to quantitative applications using metallic tracer particles in combination with optical traps, it might be worthwhile to extend our

results along the lines of [23] to take the heating of the tracer into account.

\* \* \*

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**Appendix.** – For the evaluation of  $\gamma(t)$ , we decompose  $\Delta(s, t)$  into bending eigenmodes  $\mathcal{W}_n(s)$  and mode amplitudes  $a_n(t)$ , such that

$$\Delta(s, t) = \sum_{n=0}^N \mathcal{W}_n(s) a_n(t)$$

$$\kappa \mathcal{W}_n''''(s) - f \mathcal{W}_n''(s) = \frac{\zeta_{\perp}}{\tau_n} \mathcal{W}_n(s)$$

$$\int_0^L d\sigma \mathcal{W}_n(\sigma) \mathcal{W}_m(\sigma) = \delta_{nm}.$$

The actual physical boundary conditions at the polymer ends dictate the detailed functional form of the  $\mathcal{W}_n$ . A free polymer in solution requires [24]

$$\mathcal{W}_n''(-L/2) = \mathcal{W}_n'''(-L/2) = \mathcal{W}_n''(L/2) = \mathcal{W}_n'''(L/2) = 0,$$

but the precise choice of boundary conditions is irrelevant to the following discussion. Projecting eq. (4b) onto each of the  $\mathcal{W}_n$ , we find  $N + 1$  distinct equations of motion for the  $a_n$ ,

$$\dot{a}_n(t) = -a_n(t) \left( \frac{1}{\tau_n} + \dot{x}(t) \overbrace{\langle \mathcal{W}_n(s) | 1 \rangle}^{A_n} \right) - \underbrace{\frac{\langle \mathcal{W}_n(s) | \xi_{\perp}(s, t) \rangle}{\zeta_{\perp}}}_{\xi_n(t)/\zeta_{\perp}} + \frac{\gamma(t)}{\zeta_{\perp}} \mathcal{W}_n(s_0) \Big), \quad (\text{A.1})$$

where  $\tau_n$  is the relaxation time of the  $n$ th eigenmode. The singular force term can be eliminated by choosing a complete set of allowed displacements in mode space,  $\sum \mathcal{W}_n(s_0) a_n(t) = 0$ , leading to

$$\begin{aligned} \delta_1 &= (\mathcal{W}_1(s_0), -\mathcal{W}_0(s_0), 0, \dots, 0) \\ \delta_2 &= (0, \mathcal{W}_2(s_0), -\mathcal{W}_1(s_0), 0, \dots, 0) \\ &\vdots \\ \delta_N &= (0, \dots, 0, \mathcal{W}_N(s_0), -\mathcal{W}_{N-1}(s_0)). \end{aligned} \quad (\text{A.2})$$

Combining the eqs. (A.1) of motion with the corresponding constraint equations (A.2), the dynamics of the  $a_n$  are determined completely, reading

$$M_1 \partial_t (a_0, \dots, a_N)^{\top} = M_2 (a_0, \dots, a_N)^{\top} + \dot{x}(t) V_x + V_{\xi}(t),$$

where  $M_{1,2}$  and  $V_{x,\xi}$  are given by

$$M_1 = \begin{bmatrix} \mathcal{W}_1(s_0) & -\mathcal{W}_0(s_0) & & & \\ & \mathcal{W}_2(s_0) & -\mathcal{W}_1(s_0) & & \\ & & \ddots & \ddots & \\ & & & \mathcal{W}_N(s_0) & -\mathcal{W}_{N-1}(s_0) \\ \mathcal{W}_0(s_0) & \mathcal{W}_1(s_0) & \dots & \dots & \mathcal{W}_N(s_0) \end{bmatrix}$$

$$M_2 = \begin{bmatrix} -\frac{\mathcal{W}_1(s_0)}{\tau_0} & \frac{\mathcal{W}_0(s_0)}{\tau_1} & & & \\ & -\frac{\mathcal{W}_2(s_0)}{\tau_1} & \frac{\mathcal{W}_1(s_0)}{\tau_2} & & \\ & & \ddots & \ddots & \\ & & & -\frac{\mathcal{W}_N(s_0)}{\tau_{N-1}} & \frac{\mathcal{W}_{N-1}(s_0)}{\tau_N} \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$V_x = \begin{bmatrix} A_1 \mathcal{W}_0(s_0) - \mathcal{W}_1(s_0) A_0 \\ \vdots \\ \vdots \\ A_N \mathcal{W}_{N-1}(s_0) - \mathcal{W}_N(s_0) A_{N-1} \\ 0 \end{bmatrix}$$

$$V_{\xi}(t) = \frac{1}{\zeta_{\perp}} \begin{bmatrix} \xi_0(t) \mathcal{W}_1(s_0) - \mathcal{W}_0(s_0) \xi_1(t) \\ \vdots \\ \vdots \\ \xi_{N-1}(t) \mathcal{W}_N(s_0) - \mathcal{W}_{N-1}(s_0) \xi_N(t) \\ 0 \end{bmatrix}.$$

The solution to eq. (13) then reads

$$(a_0, \dots, a_N)^{\top}(t) = e^{M_1^{-1} M_2 (t-t_0)} (a_0, \dots, a_N)^{\top}(t_0) + \int_{t_0}^t d\tau e^{M_1^{-1} M_2 (t-\tau)} M_1^{-1} (\dot{x}(\tau) V_x + V_{\xi}(\tau)).$$

Inserting the above solution into the original equation of motion (A.1), we obtain the force of constraint in mode space,

$$\begin{aligned} &(\gamma(t) \delta(s - s_0))_n \\ &= \zeta_{\perp} \partial_t \dot{a}_n(t) + \zeta_{\perp} a_n(t) / \tau_n - \xi_n(t) + \dot{x}(t) A_n \zeta_{\perp} \\ &= \zeta_{\perp} \int_{t_0}^t d\tau (M_1^{-1} M_2 + \text{diag}(\tau_n^{-1})) e^{M_1^{-1} M_2 (t-\tau)} \\ &\quad \times M_1^{-1} (\dot{x}(\tau) V_x + V_{\xi}(\tau)) \\ &\quad + \zeta_{\perp} \dot{x}(t) (M_1^{-1} V_x + A_n) \\ &\quad + (\zeta_{\perp} M_1^{-1} V_{\xi}(t) - \xi_n(t)). \end{aligned} \quad (\text{A.3})$$

The part outside the integral vanishes, except for the  $N$ th entry, which is an artefact introduced by the mode cutoff and can safely be ignored: having a finite minimum bending mode wavelength implies that even at arbitrarily short times, a finite part of the polymer will be dragged along with the monomer. We thus obtain  $\gamma(t)$  as follows,

$$\gamma(t) = \lim_{N \rightarrow \infty} \left[ \sum_{n=0}^N \mathcal{W}_n(s_0)^2 \right]^{-1} W^{\top} \int_{t_0}^t d\tau (M_1^{-1} M_2 + \text{diag}(\tau_n^{-1})) e^{M_1^{-1} M_2 (t-\tau)} M_1^{-1} (\dot{x}(\tau) V_x + V_{\xi}(\tau)),$$

where  $W = \zeta_{\perp}(\mathcal{W}_0(s_0), \dots, \mathcal{W}_N(s_0))$ . Identifying the random and the  $\dot{x}$ -dependent terms with  $\xi(t)$  and  $K(t)$ , respectively, we find

$$K(t) = W^{\top} (M_1^{-1} M_2 + \text{diag}(\tau_n^{-1})) e^{M_1^{-1} M_2 t} M_1^{-1} V_x,$$

$$\xi(t) = W^{\top} \int_{t_0}^t dt' (M_1^{-1} M_2 + \text{diag}(\tau_n^{-1}))$$

$$\times e^{M_1^{-1} M_2 (t-t')} M_1^{-1} V_{\xi}(t).$$

Note that if  $s_0$  coincides with the center of the polymer, antisymmetric modes will not contribute to  $\gamma(t)$ ; the calculation then has to be restricted to the symmetric component  $\Delta_s(s, t)$ , otherwise  $M_1$  would be degenerate. The above procedure trivially extends to an inhomogeneous stationary force profile  $f = f(s)$ . In that case, the differential operator  $\kappa \partial_s^4 - f \partial_s^2$  turns into  $\kappa \partial_s^4 - f'(s) \partial_s - f(s) \partial_s^2$ , which changes both the eigenmodes  $\mathcal{W}_n(s)$  and their respective eigenvalues, but the calculation in mode space remains unaffected.

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